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MISTLETOE INJURY TO CONIFERS IN THE NORTHWEST.[1]

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INTRODUCTION.

It is not generally known that the injury by the mistletoes to coniferous trees in the northwestern United States is such as to assume in many regions the nature of a serious forest problem. The aim of this bulletin is to point out some of the direct and indirect results of this injury. The species of trees most subject to injury are *Larix occidentalis* (western larch), *Pinus ponderosa* (western yellow pine), *Pinus contorta* (lodgepole pine), and *Pseudotsuga taxifolia* (Douglas fir). Each of these trees is attacked by a particular species of mistletoe of the genus Razoumofskya (Arceuthobium). With a few exceptions, these species very rarely occur in nature on any other than their common hosts. In the order of the above-named hosts they are *Razoumofskya laricis* Piper (Pl. I, fig. 1), *R. campylopoda* (Engelm.) Piper (Pl. II, fig. 2), *R. americana* (Nutt.) Kuntze (Pl. I, fig. 2), and *R. douglasii* (Engelm.) Kuntze (Pl. II, fig. 1).

[1] Thanks are due Mr. E. E. Hubert for assistance in the preparation of the graphs and a number of the other illustrations used in this bulletin.

GENERAL NATURE OF THE MISTLETOE INJURY.

The general nature of the injury to forest growth by these parasites principally consists sooner or later in a localization and gradual reduction of the assimilatory leaf surface of the host. As will be shown, this is caused by various burl and broom formations on the trunks and branches. The reduction of the leaf surface causes a falling off of the annual increment. During the progress of a study on the larch mistletoe in the Whitman National Forest, Oreg., in the summer of 1913, many data on the retardation of growth of its host by this parasite were assembled. More recently, in the lodgepole and yellow pine belt of eastern Washington and northern Idaho, the study was continued on these species, and at frequent intervals on the larch and Douglas fir in the Missoula region of Montana. The method of investigation was as follows: Borings from heavily infected (burled and broomed) and uninfected trees were taken with a Mattison increment borer at 4½ feet from the ground, at which point the trees were calipered. With practice the eccentricity of growth due to slope, unequal crown development, injuries, etc., may be very skillfully judged, so that it is possible to strike the pith of trees within the range of the borer with a fair degree of accuracy. In order to determine as nearly as possible the average radius, in the more doubtful cases three borings were taken. On steep slopes the eccentricity of trees may be more accurately judged than on flat land, through the knowledge that more rapid growth takes place on the downhill side of the tree. Height was computed with the Klaussner height measurer. Trees of the same species were selected as near as possible from the same type of stand and of the same general age class and the same soil conditions. Only dominant trees free from serious wounds and other possible causes of deterioration were recorded. Finding that the effects of the mistletoe on the increment of the host could be read from the last 40 years' growth of the age classes and conditions of infection selected, Table I was prepared.

TABLE I.—*The retardation of growth of forest trees caused by mistletoe, for 40 years, 1874 to 1913, inclusive.*

Host and condition.	Basis (number of trees).	Average.			
		Age class.	Height.	Diameter breast high.	Total annual growth.
		Years.	*Feet.*	*Inches.*	*Inches.*
Pinus contorta:					
Infected	50	65	35.2	6.3	0.93
Uninfected	50	60	48.5	7.8	2.93
Pinus ponderosa:					
Infected	50	100	49.5	18.2	1.54
Uninfected	50	100	77.2	22.2	5.33
Larix occidentalis:					
Infected	80	144	63.0	11.5	1.28
Uninfected	80	144	115.0	19.5	2.154
Pseudotsuga taxifolia:					
Infected	40	97	62.0	17.3	2.175
Uninfected	40	97	73.0	22.2	3.28

The results in Table I, although based on a relatively small number of trees, prove quite conclusively the effects of mistletoe on the growth of its host. They are graphically shown by the accompanying series of illustrations (figs. 1 to 4).

A glance at these graphs shows that although there is considerable fluctuation in growth, the line of the uninfected rarely falls below that of the infected trees.

These results are not at all surprising when the nature of mistletoe injury is thoroughly appreciated. In a heavily infected region, where all species and ages are more or less involved, dead, dying, or

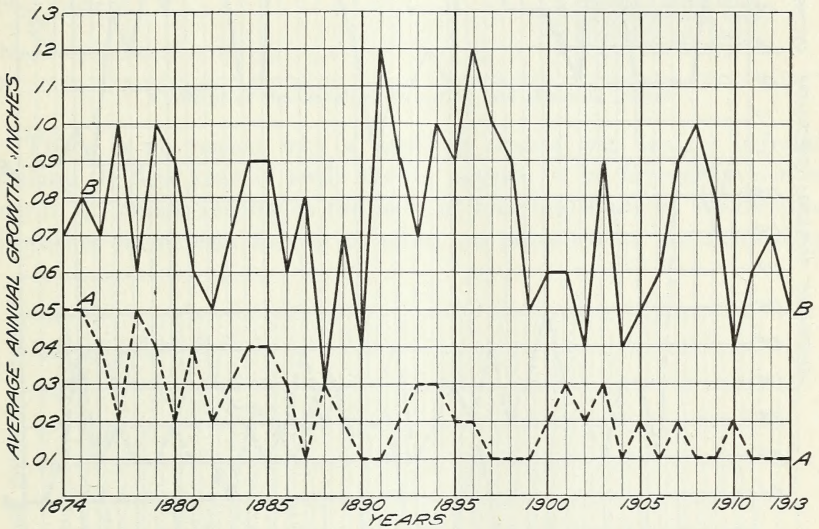

FIG. 1.—Graphs showing the average annual growth (in inches) for 40 years (1874 to 1913, inclusive) of 50 trees of lodgepole pine heavily infected with mistletoe, compared with 50 uninfected trees of the same species for the same period. *A*, Heavily infected trees: Average-age class, 65 years; average height, 35.2 feet; average diameter, breast high, 6.3 inches. *B*, Uninfected trees: Average-age class, 60 years; average height, 48.5 feet; average diameter, breast high, 7.8 inches.

weakened mistletoe trees, hastened in their decline by the inroads of fungi and insects, are a common sight. If these trees are carefully examined with respect to the average possible growth for the region, it will be found, as Table I shows, that most of them have died or have become irrevocably weakened or suppressed at a time when rapid or a normal growth should be taking place. This has been found to be true in all regions visited in the Northwest where excessive mistletoe infection is common. Infected trees of immature years, pole size and younger, may linger along indefinitely if secondary agents do not appear and may reach an advanced age, but may not attain a merchantable size. Heavily infected and, as a result of this

infection, badly stunted yellow pine, larch, Douglas fir, and lodgepole pine growing in the open and on otherwise good sites often measure less than 6 inches at the stump, but show ages ranging from 100 to 200 years or more. Young seedlings, if not killed outright within a comparatively short time after infection, usually show a

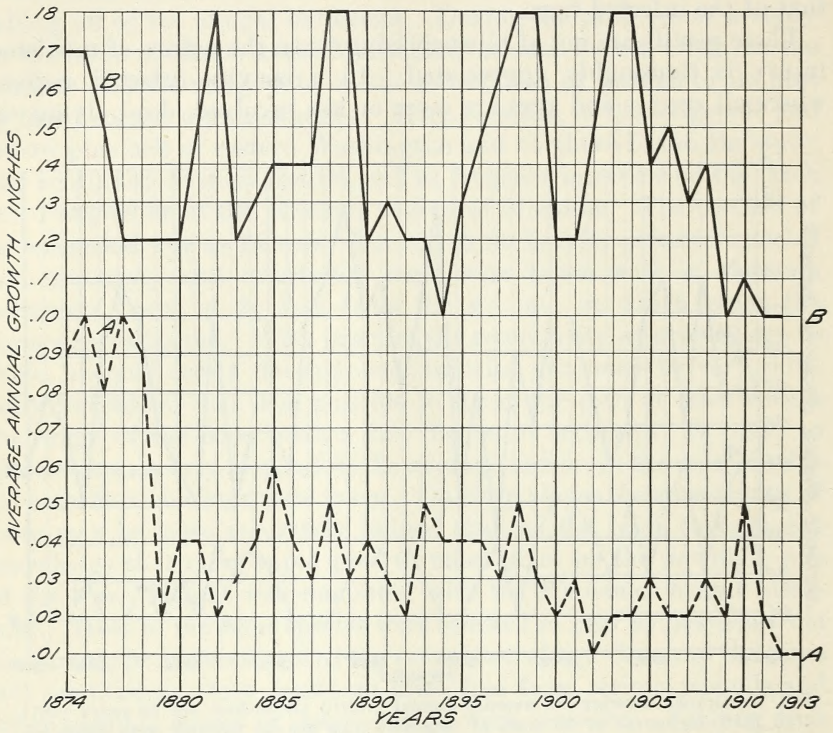

FIG. 2.—Graphs showing the average annual growth (in inches) for 40 years (1874 to 1913, inclusive) of 50 trees of yellow pine heavily infected with mistletoe, compared with 50 uninfected trees of the same species for the same period. *A*, heavily infected trees: Average-age class, 100 years; average height, 49.5 feet; average diameter, breast high, 18.2 inches. *B*, Uninfected trees: Average-age class, 100 years; average height, 77.2 feet; average diameter, breast high, 22 inches.

marked falling off of the foliar surface of the parts uninfected and finally succumb to the attack (fig. 5). Very frequently young infected seedlings develop into ball-like brooms.

Table II shows the youngest age class of five hosts at which mistletoe infection has been found to occur and the locality where the observations were made.

TABLE II.—*The youngest age class of mistletoe infection on five different hosts.*

Host.	Youngest age at which infection is known to occur.	Locality where observations were made.
	Years.	
Pseudotsuga taxifolia	4	Clark Fork Valley, Mont.[1]
Do	7	Blue Mountains, Oreg.
Larix occidentalis	5	Priest River Valley, Idaho.
Do	4	Blue Mountains, Oreg.
Do	3	Missoula, Mont.
Do	7	Sullivan Lake, Wash.
Pinus contorta	5	Spokane River, Wash.
Do	3	Blue Mountains, Oreg.
Do	6	Coeur d'Alene, Idaho.
Pinus ponderosa	5	Spokane River, Wash.
Do	3	Blue Mountains, Oreg.
Do	4	Coeur d'Alene, Idaho.
Tsuga heterophylla	8	Clearwater River, Idaho.

[1] Valleys of the so-called Bitterroot and Missoula Rivers.

There is no reason why a seedling should not become infected during its first year if seeds should happen to be favorably located upon it. Seeds falling at the base of terminal buds of yellow-pine branches have been known to effect an entrance in the succeeding

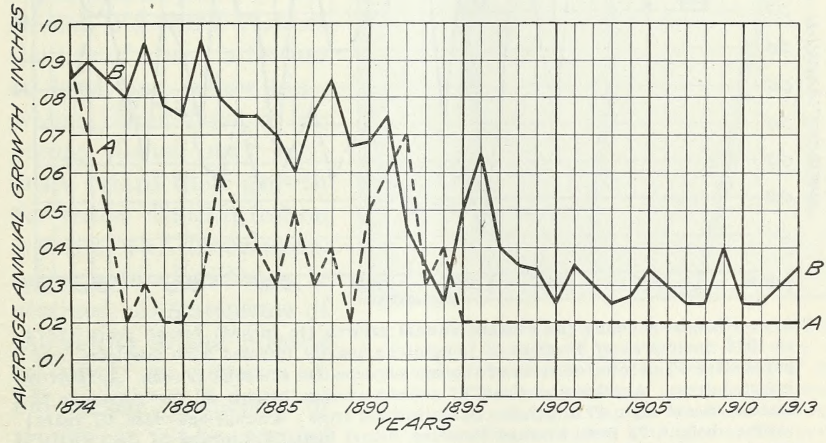

FIG. 3.—Graphs showing the average annual growth (in inches) for 40 years (1874 to 1913, inclusive) of 80 trees of western larch heavily infected with mistletoe, compared with 80 uninfected trees of the same species for the same period. *A*, Heavily infected trees: Average-age class, 144 years; average height, 63 feet; average diameter, breast high, 11.5 inches. *B*, Uninfected trees: Average-age class, 144 years; average height, 115 feet; average diameter, breast high, 19.5 inches.

season's growth within the year. All infections of firs and spruces have been found on trees ranging from 50 to 150 years. They occurred principally on the branches, resulting in large brooms, so that nothing could be determined as to the probable age of the hosts when infection took place.

No evidence is at hand to show that the primary sinker of these parasites can penetrate other than the more tender epidermis of young parts of the host. Germinating mistletoe seeds located on the smooth bark of the Douglas fir or on the irregularities of older stems of yellow pine or larch have never been observed, even after a protracted contact of the disk of the hypocotyl with the surface of the branch, to penetrate the bark. Removing the exhausted hypocotyl and carefully examining the point where the disk was attached, a barely perceptible pit or indentation is sometimes visible,

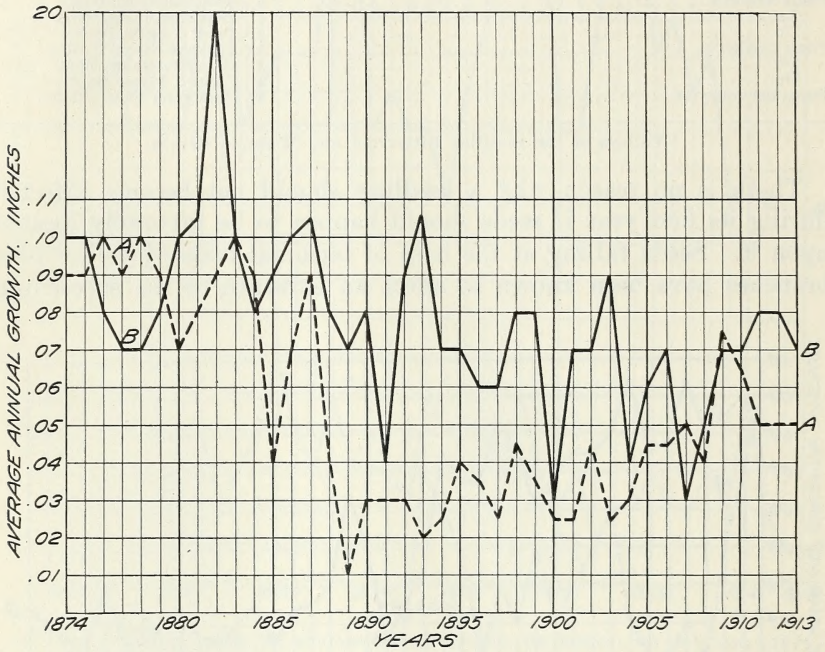

FIG. 4.—Graphs showing the average annual growth (in inches) for 40 years (1874 to 1913, inclusive) of 40 trees of Douglas fir heavily infected with mistletoe, compared with 40 uninfected trees of the same species for the same period. *A*, Heavily infected trees: Average-age class, 97 years; average height, 62 feet; average diameter, breast high, 17.3 inches. *B*, Uninfected trees: Average-age class, 97 years; average height, 73 feet; average diameter, breast high, 22.2 inches.

possibly indicating the presence of a solvent, which, however, is ineffective upon more mature bark. There is as yet no proof to support the theory of the presence of a digestive substance which enables the sinker to penetrate the bark more readily. If this were true, infection could possibly occur on older tissues, provided they were not too thick and the food supply in the seed did not become exhausted. As it is, mechanical force, supported by the nonmovable position of the seed, and irregularities of the stems, such as leaf scales, exits of leaf traces, and leaf sheaths, particularly at

the nodes and the basal scales of the terminal buds, are the chief factors in the penetration of the primary root.

The occurrence of mistletoe plants on the thick-barked branches of old trees or on the main trunk are the result of earlier infection, when the bark was thinner. What appears to be a recent infection on the older parts of trees is often merely a retarded or suppressed condition of an earlier infection which has expended most of its energy in the production of a subcortical stroma and later breaks through the bark. Periods of suppression and dominance are frequently noticeable in all mistletoes, a condition noted to be in several instances directly referable to the state of vigor of the host. An excessive flow of resin sometimes appears in the second and third year of the life of a new infection on larch and yellow pine, which, if not fatal to the young plants, may seriously retard their growth for years. Until infection by actual inoculation, using natural methods, is attained, all statements of the ability of the parasite to effect an entrance in old-barked branches or trunks can not be accepted and must be considered faulty observation. The writer has never succeeded in causing the infection of branches at any point older than four years. The ease of infection is found to be more or less in proportion to the decrease in age of the branches tested. This was proved in the case of yellow pine by inserting seeds at regular intervals in the axils of the leaf sheaths of young branches, from the terminal bud to the tenth internode. The results of this experiment are shown in Table III.

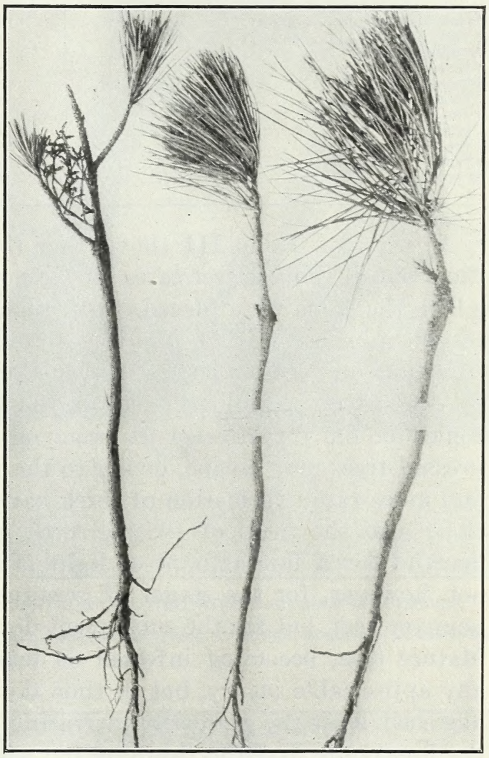

FIG. 5.—Four-year-old yellow-pine seedlings killed by mistletoe. Note the hypertrophy of the stem at the point of infection and the shortening of the needles. The two seedlings on the right were killed principally by having the wood and cambium in the swelling infiltrated with pitch. The parasite killed the seedling on the left by invading the terminal shoot.

TABLE III.—*Inoculation of Razoumofskya campylopoda on Pinus ponderosa, made in November, 1911.*

[x=Inoculation effective; 0=inoculation not effective.]

Age of part of branch tested.	Seeds sown on each internode.	Results in November, 1914, on branch—				
		No. 1.	No. 2.	No. 3.	No. 4.	No. 5.
Season's growth	10	x	x	x	0	0
1 year	10	0	0	x	x	0
2 years	10	0	0	0	0	x
3 years	10	0	0	0	0	0
4 years	10	0	0	0	0	0
5 years	10	0	0	0	0	0
6 years	10	0	0	0	0	0
7 years	10	0	0	0	0	0
8 years	10	0	0	0	0	0
9 years	10	0	0	0	0	0
10 years	10	0	0	0	0	0

A study of Table III shows that the branches were infected in three out of the five test cases on the youngest and last internode on which the seeds were placed. Infection occurred on two of the five tested branches on that part 1 year old at the time of sowing, one infection only being on the 2-year-old portion. Infection did not take place on the older parts of the branches. A tree never becomes too old for infection to occur on its youngest branches. Suppressed trees may escape, owing to the fact that slowness of growth and more rapid formation of thick bark lessens the chance of infection; also shortness of twig growth gives less opportunity. The demand for a fair amount of light is also a factor in such a case, not, however, for the stages of germination and penetration of the primary root, but for the subsequent development of the aerial parts. Mature trees becoming infected on tender branches may not suffer any appreciable injury, but in time the decline of the tree is surely hastened, since the gradually increasing hypertrophy of the branches, the breakages, and the thinning out of the foliage of the tree as a whole cause it to be greatly weakened. Almost always the result of a heavy infection on the trunk and branches of some conifers is the death of the upper portion of the crown,[1] causing staghead (fig. 6),

[1] The dying back of the crown of trees, commonly known as spiketop, or staghead, is attributed to various causes; as many, in fact, as the varied conditions under which trees grow. One of the most common theories is that on opening up a stand the admission of light to the trunk and lower crown deflects the transpiration current to the older branch orders or, as with some species, promotes the formation of a secondary crown on the main trunk. This stimulated foliar activity below reduces the water supply at the top of the crown; consequently the topmost branches die back. This is exactly what happens in the case of mistletoes. The extra crown development below, by brooming, starves out the crown above, resulting in its death. Münch (Silva, December, 1911, pp. 415–416) claims to have found a parasitic Ascomycete which causes staghead in the oak of Europe by attacking the bark and outer wood of the main shoots. The writer has found a wood-destroying fungus which attacks the upper crown branches of the chestnut in southern Indiana and causes their death. The "pencil rot," which seems to be frequently the cause of staghead in the western red cedar, is another example of fungi attacking the crown of trees. Lightning is a common cause of staghead; also injury by insects.

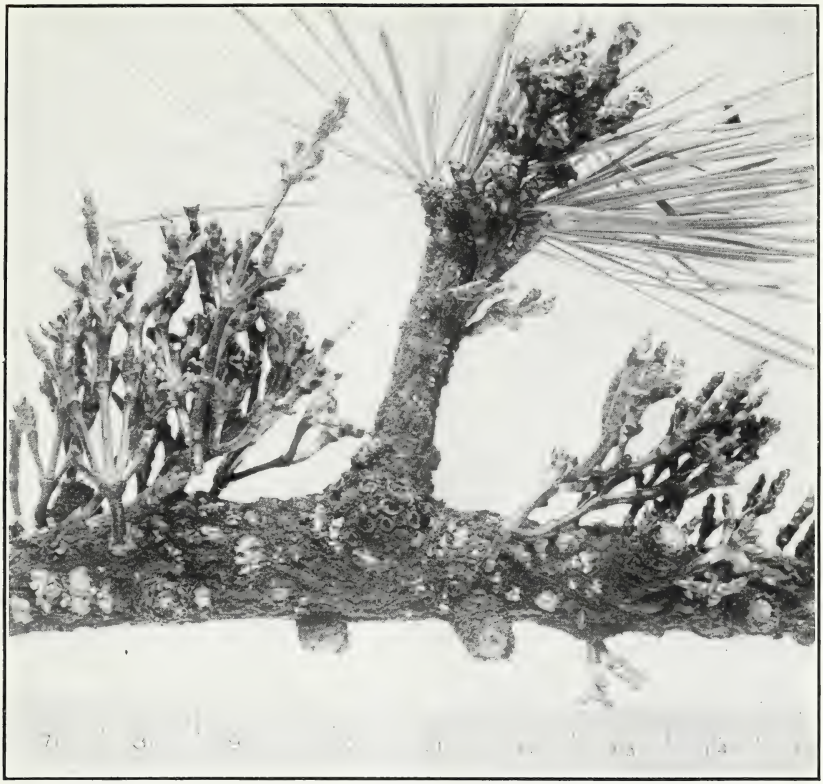

FIG. 1.—BRANCH OF LARIX OCCIDENTALIS INFECTED WITH RAZOUMOFSKYA LARICIS.
The staminate and pistillate plants are in close juxtaposition, the former at the end of the twig.

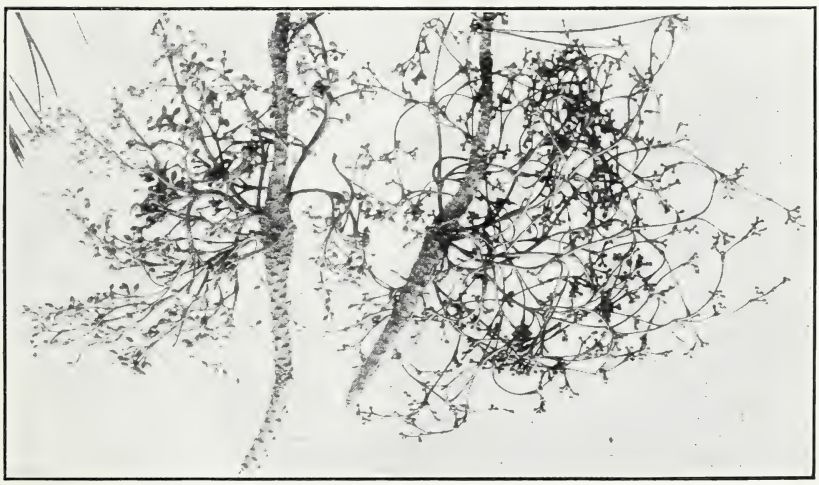

FIG. 2.—RAZOUMOFSKYA AMERICANA ON PINUS CONTORTA.
Staminate and pistillate plants; long trailing form.

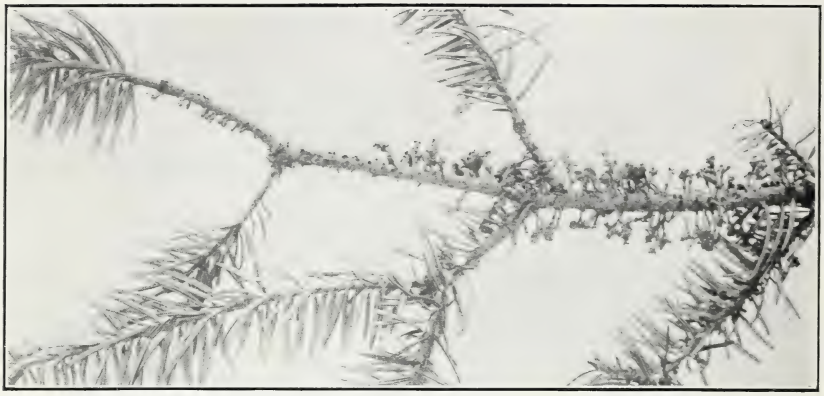

FIG. 1.—RAZOUMOFSKYA DOUGLASII ON PSEUDOTSUGA TAXIFOLIA.

Staminate plants, slightly less than natural size.

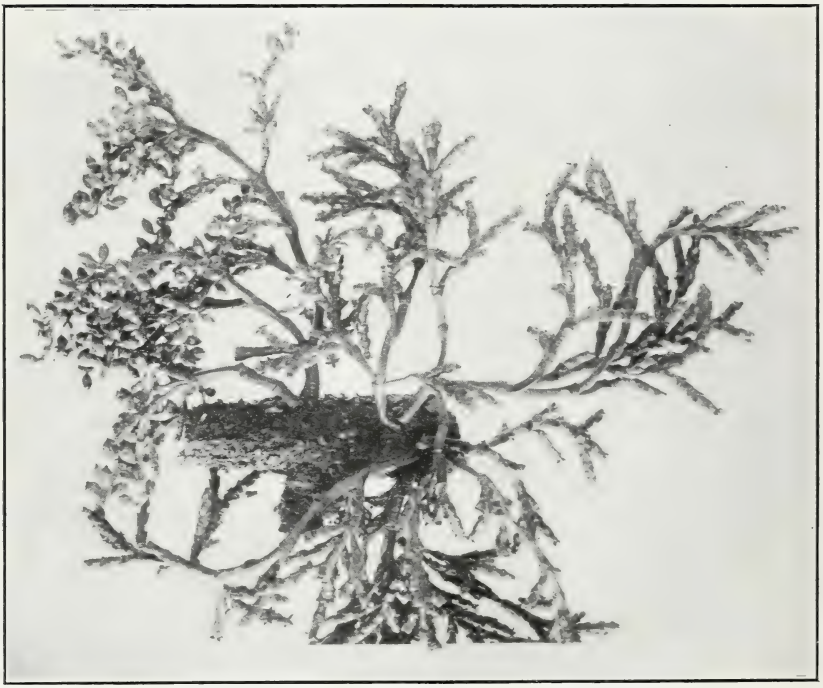

FIG. 2.—RAZOUMOFSKYA CAMPYLOPODA ON PINUS PONDEROSA.

The staminate and pistillate plants are growing close together on the same branch, a very common condition for all species, but not generally known.

FIG. 1.—AN OPEN STAND OF YELLOW PINE HEAVILY INFECTED WITH RAZOUMOFSKYA CAMPYLOPODA.

Note that some of the trees are dead and that others have very thin foliage. The structure of the dead brooms is plainly shown. Some of the trees bear burls on the main trunk. The young growth is seriously infected with mistletoe.

FIG. 2.—A HEAVY GENERAL INFECTION OF A 15-YEAR-OLD YELLOW PINE BY RAZOUMOFSKYA CAMPYLOPODA, RESULTING IN A DISTORTED AND OPEN CONDITION OF THE CROWN WITHOUT PRONOUNCED BROOMING.

The natural excurrent growth of the main trunk is entirely changed.

FIG. 1.—NEEDLES OF DOUGLAS FIR FROM A NORMAL BRANCH (AT THE RIGHT) AND OF A MISTLETOE BROOM ON THE SAME TREE, SHOWING THE DIFFERENCE IN SIZE.

FIG. 2.—YELLOW PINE AT THE HEAD OF A CANYON, SHOWING MISTLETOE INFECTION.

Note that the heaviest infection occurs on the immediate edge of the canyon and that the intensity of the infection decreases as the distance from the brow of the canyon increases; also that the upper crowns of the infected trees are becoming very thin.

or in some cases the entire tree may succumb (fig. 7 and Pl. III, fig. 1.) In many parts of the Whitman National Forest, wherever the heaviest infection of yellow pine occurs the percentage of dead or spiketopped trees reaches a comparatively high figure.

In a report to Supervisor Ireland, Ranger Smith, in referring to the seriousness of the infection of yellow pine in the vicinity of Susanville, Whitman National Forest, states that since 1907, the year in which the mistletoe damage in the region first received attention, the infection of all age classes has been growing worse, probably 40 per cent of the stand now being infected. Of the more mature stand, approximately twice as many trees near the station as were noted in 1907 have since died. Ranger Smith further states that for a most pronounced general infection of all species the drainage basin of the South Burnt River particularly illustrates the devastating effects of mistletoes. "Almost every yellow pine from seedlings up and Douglas fir above sapling size is heavily infected and most of the mature timber shows great retardation of growth and is now adding little or no increment. This infection covers a large part of the best yellow-pine sites in the yellow-pine belt of this watershed." This region was not visited by the writer, but to judge from studies in other parts of the same forest Ranger Smith's observations are undoubtedly correct.

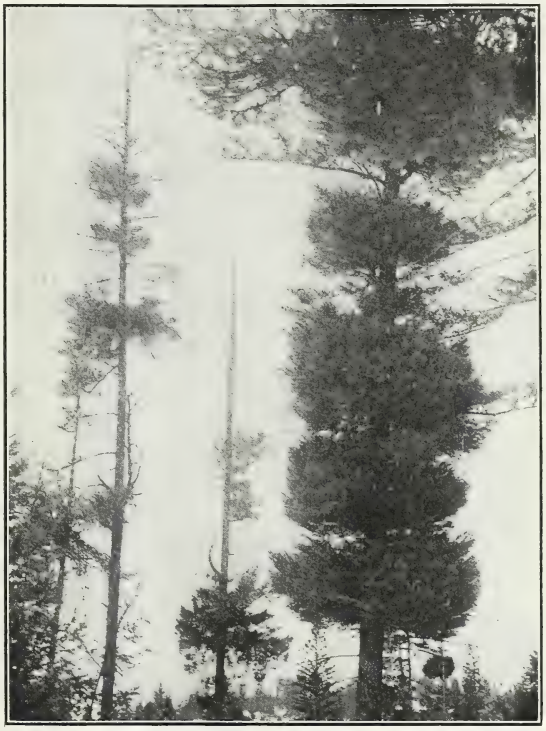

FIG. 6.—Douglas fir, showing the death of the upper portion of the crown caused by *Razoumofskya douglasii*. The tree to the right with the series of immense brooms also has a dead top. A large broom had split off from the trunk of the tree on the left. All the young growth in the vicinity of these trees is seriously infected.

In order to determine the relative amounts of different species cut as snags on the W. H. Eccles Lumber Co. sale (Whitman Na-

tional Forest), the following figures were assembled by Mr. T. J. Starker, covering a period of 28 days of cutting:

Western larch	556
Western yellow pine	1,221
Douglas fir	422
Total	2,199

It must not be assumed that the death of these trees resulted from mistletoe. It is doubtful whether the death of even a small percentage of them, with the exception of the larch, can be so referred. A more conservative statement would be that mistletoe had a large share in their death by causing spiketop, the brooming of branches, and the formation of burls on the trunk. These are common forms of mistletoe injury for all three species in this region and lead up to serious insect infestation, of which more is said later. That mistletoes are capable of actually causing the death of their hosts is first shown by their effects on young growth from three to eight years old. In a heavily infected but very open stand of yellow pine on the bench lands of the Spokane River, Wash. (Pl. III, fig. 1), an attempt was made to ascertain the amount of injury resulting to the seedlings of an average sample acre, which included in its area nine semimature and heavily infected trees in all stages of suppression. The acre was divided into plats and all young growth counted and examined as to infection and the condition of the infection. The number of seedlings and small growth below 8 feet in height totaled 480, which is an excellent reproduction for this region. Just a little more than half of this number, or 245, were found to be infected, representing every possible type of infection on stem and branch. It is not to be expected that these seedlings would ever grow up to form merchant-

FIG. 7.—Douglas fir killed by mistletoe. Note the total absence of normal branches. The structure of the brooms is here plainly shown. Note the straight trunk of the larch in the background. It is uninfected by mistletoe and still retains its original branches.

able trees. Considering the severity of the infection, they could not be expected to attain near the size of their parents shown in Plate III, figure 1, and from which they received the mistletoe. Of the 245 infected seedlings, 49 were dead. An examination of the root system of each seedling showed it to be well developed. In the absence of any other deteriorating influence except an occasional needle infested by *Chionaspis pinifolia* Fitch, the death of these seedlings must be ascribed to the luxuriant growth of mistletoe which they had supported (fig. 5). In most cases the tufts of mistletoe had fallen away. The bark of the large fusiform swellings was usually ruptured and both the wood and bast tissues were so heavily infiltrated with pitch that the passage of food materials between the crown and the roots was wholly impossible, resulting in death. In this respect there is a parallel between this type of mistletoe injury to seedlings and that resulting from the perennial mycelium of some caulicolus Peridermiums.

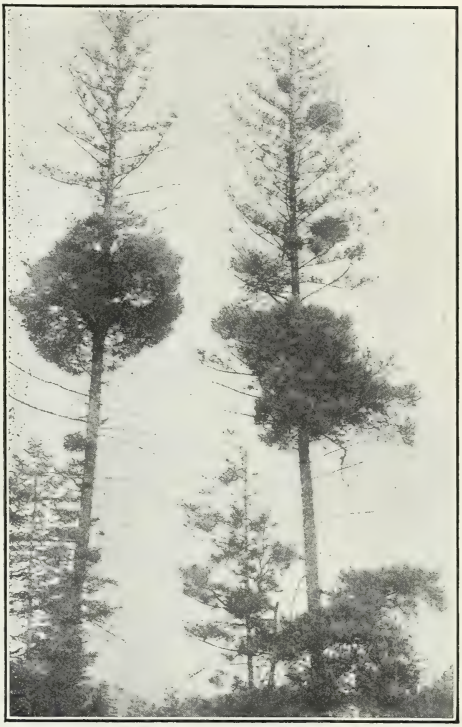

FIG. 8.—A group of Douglas firs with their entire lower crowns developed into brooms by *Razoumofskya douglasii*. Note the sparse foliage of the upper crowns and the young brooms in the tree on the right, showing how the parasite travels upward. The branches between the brooms have died from lack of nourishment.

A further study of the large trees shown in Plate III, figure 1, is illuminating. Two of them, the right and the left in the figure, are dead. Scarcely a single normal branch is to be seen, but instead are numerous large gnarled and distorted brooms. These trees measured on an average 9.3 inches in diameter at 4½ feet from the ground, and increment borings showed the age of each to be 190 years. This is far below the diameter of normal trees of the same age for the region. A careful search for secondary causes of injury resulted negatively. The trees were absolutely sound. Lightning injury, which sometimes causes spiketop in yellow pine and other conifers and which sometimes is erroneously attributed to mistletoe, was not present. With the evidence in hand, it is safe to state that the trees

were killed by the parasite. The other trees in the figure show various stages of suppression and an abnormal thinness of foliage. The tree on the extreme right shows midway on its trunk a typical mistletoe trunk burl.

It is often disputed that mistletoe is a cause of spiketop or that it is totally unknown for some species. The first and heaviest seat of infection in nearly all trees of economic importance is in the lower part of the crown (figs. 6 and 8). This is not necessarily a result of the seeds of the parasite falling first on the lower branches, but is rather the result of the fact that the main shoot continues for a time to grow in height, and the crown may attain its normal height before the effects of the parasite become dominant. The mistletoe spreads upward from the lowermost branches, with the result that the more recently formed branches are continually being infected. That these infections may not cause a brooming of the branches in the beginning is abundantly shown by the entire absence of any brooming on young infected branches of several host species. This, however, is only the first stage in the hypertrophy of the branch. After the lapse of several years, typical brooms are formed. With the increasing hypertrophy of the lower portion of the crown, food materials are more and more appropriated at this point. The result is a drain on the resources of the entire tree to support the brooms. Materials traveling upward from the roots are likewise utilized by the broomed branches, with the result that the upper portion of the crown starves and in cases of severe infection finally dies (figs. 5, 6, 7, and 8). Spiketop is an almost universal condition in heavily infected larch. The tendency to form spiketop in this species, however, is greatly augmented by the brittleness of its branches. Douglas fir probably comes next in order of frequency of dead tops resulting from the growth of mistletoes. The condition is common for yellow pine in all regions where observations have been made by the writer and is reported to be of frequent occurrence by correspondents in Utah and Wyoming. Lowland and mountain hemlocks, when heavily infected, quite commonly exhibit dead tops. An unusual case of heavy infection of the former species was studied in the St. Joe National Forest. Practically every tree in the entire stand was dead in the top (fig. 9). Lodgepole pine is less affected in this manner than any other conifer so far studied by the writer except spruce and fir. The last-named species are so seldom infected, however, that they would not enter into the discussion.

There can be little doubt that spiketop is very often the result of heavy mistletoe infection, but varies in degree for the several hosts. This condition is of importance, since the proportion of snags in the stand is thereby increased, which may promote injury by fungi and insects; it also increases danger from lightning fires.

With the conclusion of this general statement of mistletoe injury a more detailed discussion of the various types of infection will now be taken up.

RESULT OF INFECTION ON THE BRANCHES.

One of the first effects of infection, either of stem or branch, is the formation of a fusiform swelling (fig. 10). Sometimes this swelling is very pronounced and may resemble the enlargements caused by some species of Peridermium (fig. 11). The swelling is the first stage of the future hypertrophy commonly known as witches'-brooms. The absence of any pronounced brooming from early infections has led some observers to the conclusion that brooms are never produced on some conifers. Any change from the normal branching is here considered a broom. Still it is not necessary to draw such sharp lines, as the brooms produced by all mistletoes of the genus in question are quite typical. It may require several years for the broom to form. If young trees are generally infected they sometimes assume an open, ragged appearance, which to the casual observer would not be considered a broom (Pl. III, fig. 2). Nevertheless, the tree is no longer excurrent. A similar condition is sometimes noted in more mature larches, where the infection is so generally distributed throughout the entire crown that no typical brooms are produced for years. Heavily infected branches of old trees of all species are seldom without brooming of some kind, and in most cases typical brooms are formed. The mistletoe plant may die out entirely on very old brooms, especially those of yellow pine

FIG. 9.—Western hemlock (*Tsuga heterophylla*) infected by *Razoumofskya tsugensis*. These trees do not possess a single normal branch. All are broomed. The trees in the background are spike topped. The tree in the foreground has had its growth in height arrested by an immense terminal broom.

(fig. 12), but the stimulus to abnormal branching may continue. Brooms are formed on all hosts attacked by this genus of mistletoe.

FIG. 10.—Young, first infections of *Razoumofskya campylopoda* on western yellow pine (*Pinus ponderosa*).

Those of the yellow pine, owing to their loosely branched condition (fig. 12), are sometimes not as conspicuous as those produced on Douglas fir (figs. 6, 7, and 13), larch (fig. 14), hemlock (fig. 9), or lodgepole pine.

In all the regions where the yellow-pine mistletoe has been observed in the States of Washington, Oregon, Idaho, Montana, and South Dakota, brooming is a common result of the growth of the parasite on this tree. Correspondents in Wyoming, Utah, and Colorado report that old infected trees are seldom without them. MacDougal (8)[1] refers to the excessive brooming of yellow pine by mistletoe in the Southwest. Meinecke (10) refers to the very conspicuous brooms on Jeffrey pine, sugar pine, yellow pine, lodgepole pine, and Douglas fir.

FIG. 11.—A larch branch, showing the result of a first infection at its base by *Razoumofskya laricis*. This is the beginning of a burl at this point, which will spread to the main trunk.

The old brooms of the Douglas fir, because of the long, trailing, willowlike branches of the lower portion of the broom, are more conspicuous than those of other conifers (fig. 13). They sometimes attain an immense size, often including the entire crown (fig. 6). In

[1] Reference is made by number to "Literature cited," p. 39.

most cases brooms are initiated on the Douglas fir soon after infection. Young seedlings frequently die in the top, owing to the formation of a lateral broom midway on the stem. In the heavily infected regions of Montana, especially in the Clark Fork (Bitterroot and Missoula Rivers) drainage, brooming of the Douglas fir is so universal and of such extent that scarcely a single infected tree is free from brooms of some type (figs. 6 and 7). The structure of these brooms is very plainly shown if the tree succumbs to the parasite, as it often does (fig. 7). The formation of brooms invariably results from mistletoe infection on the western larch. They may be situated on any part of the branch or at its base (fig. 14). In the latter case the entire branch eventually dies or is broken off by the wind, and its place is usually taken by a series of short, scrubby secondary branches forming a trunk broom. This broom eventually dies, leaving a large knotty burl of serious consequence not only to the life of the tree but greatly decreasing its value for lumber. Excessive brooming is a common feature wherever infected larch occurs and is the chief cause of injury to the species. In some localities in the Blue Mountains of Oregon and parts of Idaho and Montana, where this mistletoe is common, a normally formed larch is seldom found. Instead of the symmetrical, conical crown so characteristic of the normal tree, the crown develops under the influence of the parasite into a denuded spike, bearing only a few ragged branches. When it is recalled that practically every larch in these regions, from pole size up, is more or less infected and seldom attains a normal size, in many cases being killed outright, some notion may be had of the seriousness of the effects of the parasite on its host.

FIG. 12.—Typical broom on yellow pine caused by *Razoumofskya campylopoda*. Note that the end of the branch is dead.

The brooming of the branches of the lodgepole pine by mistletoe is as characteristic as for the other hosts mentioned. Frequently the entire tree is involved, but more often only the lower branches. A few instances have been noted where the parasite hung in long festoons from the several infected branches

FIG. 13.—Typical broom of the weeping-willow type on Douglas fir caused by *Razoumofskya douglasii*. Note the long, flowing branches. Sometimes these branches are 8 to 10 feet long.

FIG. 14.—Typical brooms of old infections on western larch caused by *Razoumofskya laricis*. Very few of the original branches remain, and they are heavily broomed and covered with lichens. The old branches are replaced by short scrubby secondary branches. Note that two of the original branches still remain, but are dead.

without any particular hypertrophy of the branch as a whole. This condition is more apt to occur in dense stands. Observations by the writer on *Picea engelmanni*, *P. mariana*, *Abies grandis*, *A. lasiocarpa*, *A. concolor*, *A. magnifica*, *Tsuga heterophylla*, *T. mertensiana*, *Pinus monticola*, *P. albicaulis*, *P. flexilis*, *P. attenuata*, and other conifers show that brooming of the branches is a common phenomenon attending mistletoe infection of these species.

The weight of these brooms on many conifers is frequently sufficient under stress of winds and rain to cause the branches to split from the trunk, or to break farther out if the brooms are located far out from the trunk. This very commonly occurs in the case of

yellow pine and Douglas fir (fig. 15) and is the rule for larch. The stunting effect of these brooms on the trees as a whole was in one instance very interestingly shown by the fact that a middle-aged Douglas fir increased the radial dimensions of its annual rings after the removal by the wind of an immense broom located midway on the trunk. The weight of the brooms on some conifers is very often greatly increased by the accumulation of dead needles, lichens, etc. (fig. 14). When loaded with snow or saturated with moisture the brooms are more easily broken off by high winds. The ground around the base of heavily infected larches is very frequently littered with brooms broken off in this manner, often insuring the death of the tree in case of ground fires. During the early part of October, 1914, an unusually heavy fall of soft snow occurred locally over a small area around Missoula, Mont. The snow accumulated in such quantities on the mistletoe brooms of the larches and Douglas firs throughout the area that the ground around the more heavily infected trees was piled high with fallen brooms.

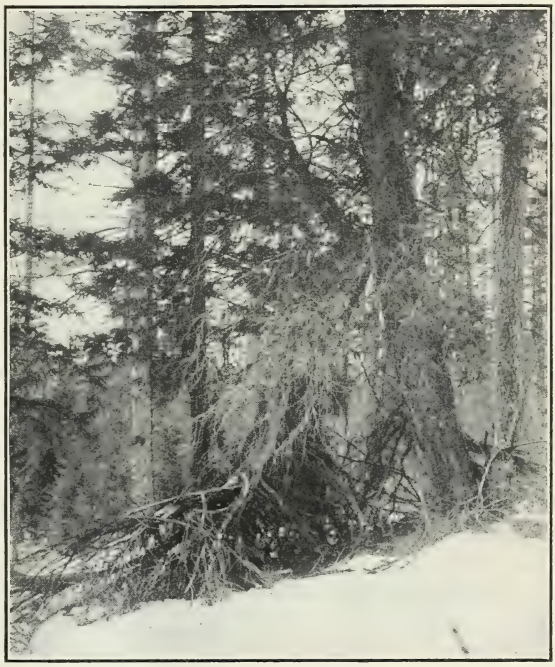

FIG. 15.—Fallen brooms split from the trunk of a Douglas fir and piled about the base of the tree—a serious fire menace.

The foliage of old and mature mistletoe brooms is usually not as long lived as that of normal branches of uninfected trees. This is not true in the case of young well-nourished brooms. It has been observed to any extent only in old brooms which have begun to tax the food supply of the tree or the branch on which they are located. In the course of one year it was determined that 655 more needles fell from a small but mature broom on a Douglas fir than from a normal branch of a neighboring uninfected tree of the same species. The number of needles falling from the broom totaled

976, from the branch 321. On very old brooms of the western larch it is often noticed that the needles begin to turn yellow some time before those on the branches of uninfected trees. Exactly the reverse may occur in the case of recently formed brooms, owing to the larger amount of newly stored food materials in the swelling on the main branch and the branches of the brooms. That the broom may be the cause of a great localization of food substances is indicated by the fact that in heavily infected Douglas fir and larch the last part of the tree to succumb is usually the smaller and younger brooms of the tree. Frequently trees of these species are noticed with only a single small broom living, the rest of the branches being apparently dead; likewise the old and exhausted brooms. The increase in the number of needles on the broom due to the multiplication of its branches is usually at the expense of the needle development on the normal parts of the tree. For this reason an excess of food materials for the tree as a whole does not take place. The foliage beyond the broom becomes thin and, in most cases, the end of the branch dies (figs. 12 and 14). The food materials are entirely stored and appropriated by the broom itself. The phenomenon is analogous to the formation of spiketop of the main trunk.

That brooms do not always necessarily mean an increase in foliar surface for the host, since we have seen that parts of the branches not supporting brooms frequently die, is shown by a comparison of the needles of old brooms with those of normal branches either of the same tree or of uninfected trees. Such a study was made in the case of the Douglas fir. It was found that the needles of the brooms on the trees studied were uniformly a little less than one-half as long as the leaves of the normal branches (Pl. IV, fig. 1). Neither were they as thick or as broad. By compensation it would be possible to determine approximately the actual foliar surface of a given broom and compare it with that of a given normal branch of the same whorl and of the same age. This difference in the size of the needles was found to hold good only in the case of old, mature brooms of trees which were beginning to be suppressed. Young brooms, especially on young trees from 10 to 20 years old, often have abnormally long needles on the still upright branches, but this condition is not long maintained. Soon these branches begin to droop, the broom becomes denser, the needles disappear from the center outward, and they are often sparingly distributed along the stems but more densely assembled on the last few years' growth (fig. 13). With continued suppression of the Douglas fir and exhaustion of the broom, a new type of branching often appears. The long trailing, weeping-willow-like branches cease to elongate and the cortical stroma of the parasite is enabled to catch up with the terminal bud and kill it. The branch

ceases to grow in length and instead forms abnormally abundant lateral branches. The terminal buds of these are likewise overtaken by the parasite, resulting in additional lateral branches, and so on, until a type of dichotomous branching results. This is more noticeable in the compact type of broom than in the long, trailing type, but is quite common in both, especially on exposed and wind-swept areas.

A very interesting hypertrophy of the foliage spurs is often shown by the brooms of the larch. The spurs are frequently abnormally large and may be four or five times as long as those of normal branches (fig. 16). On such spurs the needles are usually shorter and sparingly clustered. Eventually the parasite enters the spur and kills it. Not infrequently a mistletoe plant is found growing out at the apex of the spur or from its side, causing great distortion and the total disappearance of the needles, and eventually the death of the spur. The reduction of foliage by the thinning and shortening of the needles of the trees as a whole, and of the brooms sooner or later, is characteristic of mistletoe infection on all hosts.

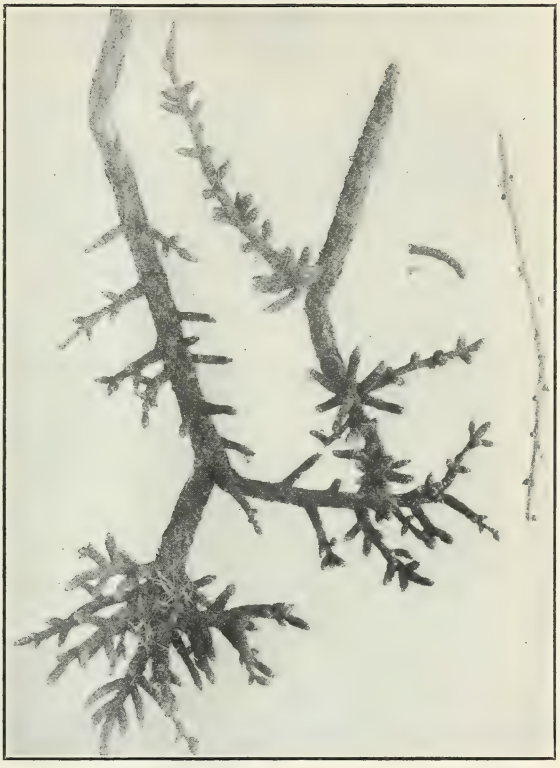

FIG. 16.—Abnormal foliar spurs of the western larch caused by *Razoumofskya laricis*. Note their size as compared with normal spurs.

The food material, which undoubtedly is accumulated in the brooms, seems to be entirely appropriated at these points and does not serve the host as a whole. The support of the excessive number of branches is necessary, but the parasite itself undoubtedly appropriates a large share at the expense of the healthy branches. The yellow-pine mistletoe has been observed to become more luxuriant and to develop abnormally long stems on swellings which had been lacerated or gnawed by rodents. Evidently the accumulation of

extra food materials in the healing tissues at this point exercised a beneficial influence on the parasite.

The actual nutritive relation between these parasites and their hosts is not at present well understood. The constant removal of all the needles of six lodgepole pines 8 to 12 years old on which large clumps of mistletoe were attached has not in the second year of the experiment resulted in the death of either the host or parasite. The controls, viz, six young pines of the same age, stripped of their needles but bearing no mistletoe plants, have died. This experiment indicates a possible transfer between the host and parasite not only of water and inorganic salts, but of organic food materials as well. However it may be interpreted, it seems that the pines were kept alive temporarily by the mistletoe. Probably it is a mutual subsistence on stored materials. It must be remembered that the whole tendency of the activities of these mistletoes (*Razoumofskya* spp.) is to reduce the life functions of the host to their lowest point, and this is the fact that should be of chief concern to the forester.

FIG. 17.—Area on the main trunk of a yellow pine infected by *Razoumofskya campylopoda*. The rough, irregular bark indicates the location of the burl tissues. A few short mistletoe plants not visible in the illustration were present.

RESULT OF INFECTION ON THE TRUNK.

Another form of mistletoe injury results when infections occur during the early life of the tree, with the formation of burls on the trunk. No case is on record of any member of the genus Razoumofskya effecting an entrance to its host through the mature cortex. If apparently recent infections on old parts of trees are carefully examined, the mistletoe plant will be found to have persisted from the time when the branch or trunk was young. Until it is proved by actual inoculation that the parasite is able to penetrate the mature cortex with its outside covering, commonly called the bark, the foregoing statements must remain valid.

Burls on the trunk caused by mistletoe are very common for some hosts, but vary in frequency on others. In point of frequency the western larch is most seriously affected by this kind of injury. Two types of burls occur on this tree, determined by the nature of the original infection. If the infection occurs at the base of a branch (fig. 11) and travels to the main trunk, a basal branch burl results, giving rise to a broom, which later dies, leaving a great burl, often of large proportions. If infection occurs directly on the main trunk the beginning of a trunk burl is immediately initiated. With

the increasing age of the host the burl tissues radiate outward in a fan-shaped area when viewed in cross section and soon leave an open wound, through the death of the central part of the infected wood. These two types of burl are so common on larch in mistletoe regions that the quality of the wood is seriously injured, resulting in a large amount of cull. In the several regions studied by the writer mistletoe burls on yellow pine are frequent. In one section of the city park at Coeur d'Alene, Idaho, are 30 or 40 large, old yellow pines. About half of the trees have mistletoe burls on the first

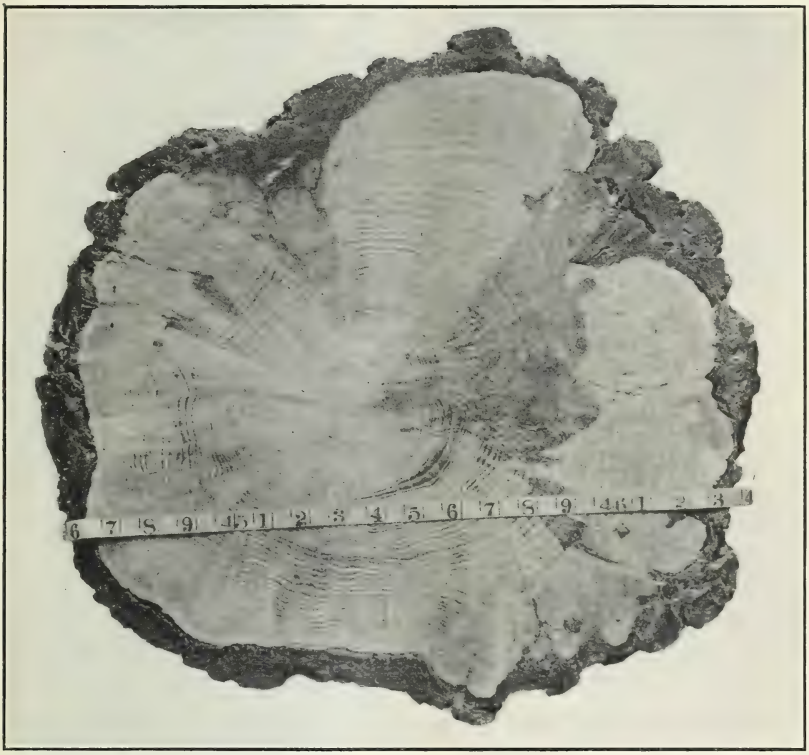

FIG. 18.—Cross section of a mistletoe burl on the yellow pine shown in figure 17. (The tape shows feet in tenths.)

log length and in most cases the parasite is still living in them, with a few scattering short aerial parts. Similar conditions prevail throughout the Spokane River Valley and around Coeur d'Alene Lake. Mistletoe burls on old yellow pine may or may not be conspicuous. Frequently there is no pronounced swelling (fig. 17) and sometimes the only means of detecting the diseased condition is by the presence of the mistletoe or an unusual roughness of the bark. A section through the tree at this point, however, shows the curly grain and the old roots of the parasite extending to the point of original infection (fig. 18). These burls are often very conspicu-

ous, large barrel-shaped swellings, from which pitch usually exudes in large quantities. Infection on one side of the tree generally results in the type of burl shown in figure 19.

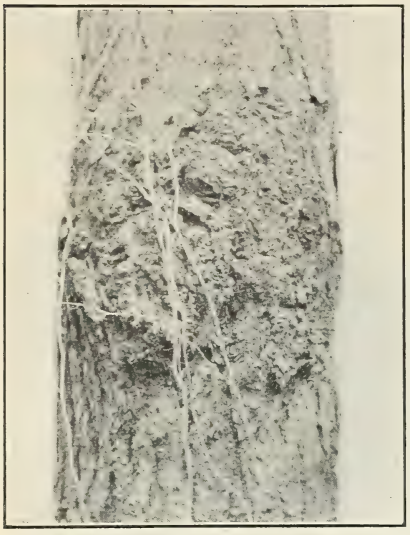

FIG. 19.—Common type of burl on yellow pine caused by *Razoumofskya campylopoda*. The tree is 3 feet in diameter at this point.

Burl formations resulting from mistletoe are a common feature on western hemlock wherever the parasite occurs in quantity. The same is true for the mountain hemlock. In the Marble Creek region of the St. Joe National Forest mistletoe burls on the hemlock are of frequent occurrence. Allen (1, p. 20–21) writes of this type of injury as follows: "If, however, the plant gets foothold on the leading shoot, a burl follows which persists throughout the life of the tree and not only ruins a log, but renders the tree apt to be broken by the wind." Infection on the main trunk of lodgepole pine is often attended by long fusiform swellings as the parasite progresses from the original point of infection. This may continue until the bark becomes so hard that the plants can not push up through it and the spread of the parasite ceases (fig. 20). The parts

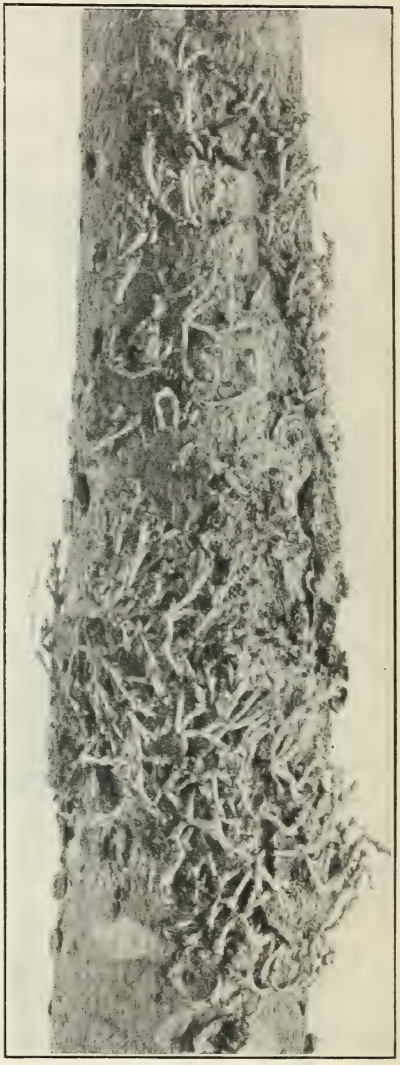

FIG. 20.—Main stem of a lodgepole pine infected by *Razoumofskya americana*. Note the spread of the parasite from the original point of infection. The bark at this point very frequently dies, leaving an open wound. (Photographed by George G. Hedgcock.)

infected, however, may continue to produce aerial branches of the mistletoe to a very advanced age. True mistletoe burls are probably of less frequent occurrence on Douglas fir than on any other economic tree species. Burls do occur, however, with sufficient frequency to be characteristic of mistletoe infection on the trunk of this tree. Large elongated mistletoe burls, including the entire circumference of the trunk, occasionally occur in heavily infected trees in many parts of Idaho and Montana (fig. 21). More frequently there is a series

FIG. 21.—Large mistletoe burl on Douglas fir caused by *Razoumofskya douglasii*. This burl is approximately 10 feet long and 2 feet in diameter at its widest part.

FIG. 22.—A Douglas fir, showing numerous burls caused by *Razoumofskya douglasii*. The branches are heavily broomed. A high degree of infection, but a common condition, is shown.

of individual burls, more or less confluent, on one trunk (fig. 22), each burl representing the seat of an old infection, from which the aerial parts of the parasite have long since disappeared. Longitudinal and cross sections through these burls show the characteristic fan-shaped areas of infection (fig. 23). In numerous cases the burls originate from infections at the base of branches. If the branch dies or is broken off, an open wound is formed in the center of the burl. Very peculiar swellings or small burls frequently occur on

the branches of brooms. These are sometimes so numerous as to cause the branch to resemble a chain of spherical balls. Mistletoe infection on the trunks of spruces in the East often results in the formation of burls; also on the western firs. It can be safely stated that swellings and distortions of the main trunk which persist throughout the life of the tree are a characteristic feature of mistletoe infection on most conifers of economic importance.

The spread of the burl tissues tangentially and longitudinally, which, as previously indicated, are frequently inhabited by the

FIG. 23.—Cross section of one of the burls on the Douglas fir shown in figure 22. This section does not pass through the point showing the age at which the infection first occurred. (The tape shows feet in tenths.)

parasite until a very advanced age,[1] results, as is the case with most species, in cutting off the transporting tissues and hastens the decline of the tree (figs. 20, 23, and 24). The bark and wood of the

[1] Meinecke, in 1912 (9, p. 38), records the age of a mistletoe plant (*Phoradendron juniperinum libocedri* Engelm.) at approximately 230 years. Species of the genus Razoumofskya are likewise capable of maintaining themselves to a very advanced age. One instance recorded by the writer may be cited of *Razoumofskya campylopoda.* A cross section through a mistletoe burl of this species, 3 feet from the ground, on yellow pine—a position precluding any but an original infection at an age when the bark was thin—showed that the parasite had continuously lived in the burl tissues for 340 years. The old roots, now dead except those immediately next the cambium, could be readily traced to the point of original infection The age of the tree at this point was three years. The burl bore a single fertile aerial branch of the mistletoe. The greater mass of the cortical stroma was entirely without aerial parts, indicating the remarkable condition of parasitism first pointed out by Meinecke for *Phoradendron juniperinum libocedri.*

outer central area of the burl die soon after the death of the cortex, especially in burls on the larch, and open wounds are formed, inviting the attack of forest-tree insects and wood-destroying fungi (fig. 24). The abnormal thickness and the soft, spongy consistency of the inner bark of mistletoe-infected branches are attractive to various gnawing animals; they are also an index of the storage of food materials at this point (fig. 25).

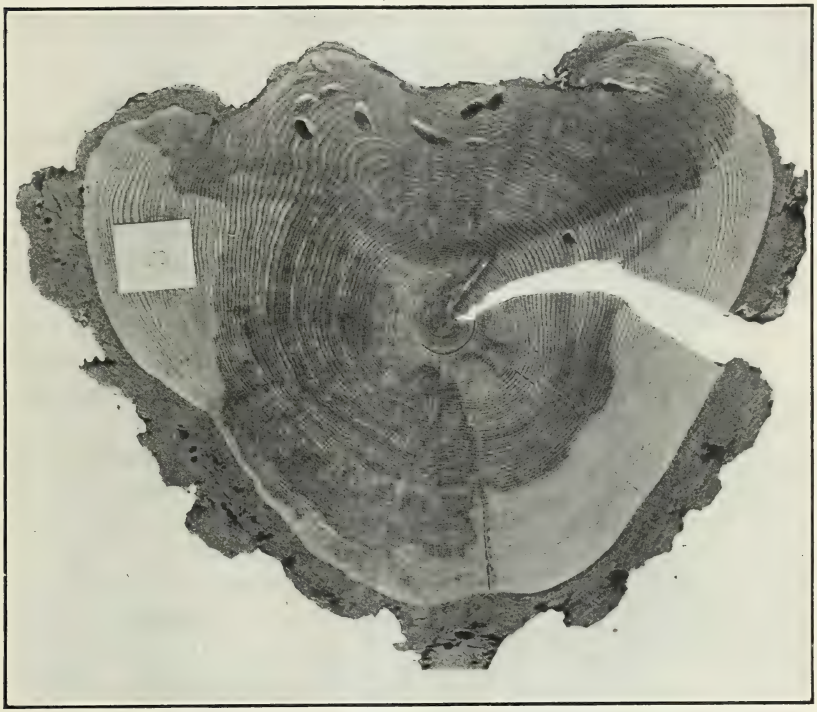

FIG. 24.—Cross section of a burl on a western larch caused by *Razoumofskya laricis*. Diameter of burl, 2 feet. Note the presence of borers and fungi. The check appeared in seasoning.

RELATION OF MISTLETOE INJURY TO FUNGOUS ATTACK.

Some very interesting data have recently been assembled by the writer on the relation of mistletoe burls to fungous attack. From cutting areas on the dry bench lands of northern Idaho, 540 mistletoe-infected living larches were examined. Out of 600 mistletoe burls found on these trees, 278 were inhabited by serious wood-destroying fungi and other unimportant species. According to frequency of occurrence the most important of these fungi are *Trametes pini* (Brot.) Fr., *Fomes laricis* (Jacq.) Murr., *Polyporus sulphureus* Fr. (four occurrences at 20 feet up on the trunk, a very

unusual habitat), *Trametes serialis* Fr., and *Lenzites sepiaria* Fr. *Fomes pinicola* Fr. was found rotting the heartwood of living trees in three different cases and had entered its host through mistletoe burls 10 feet from the ground. *Polyporus volvatus* Pk. occurs frequently on the burls of larch and yellow pine. Several species of Thelephoraceæ were collected from the mistletoe burls, chief of which were *Stereum sulcatum* Burt, *Corticium berkeleyi* Cooke, *C. galactinum* (Fr.) Burt, and *Peniophora subsulphurea* (Karst) Burt. *Ceratostomella pilifera* (Fr.) Wint., the bluing fungus, appeared occasionally in the dead wood of the burls. *Trametes pini* affected 80 per cent of all burls attacked by fungi. Since the most advanced stages of decay were always at the burl or in its near vicinity, it was assumed that the fungi had entered at this point. The decay at or in the burl tissues was in most cases not connected with the decay which is often present in other parts of the trunk. The breakage of old branches possessing heartwood, through the accumulation of brooms at their outer extremities, is likewise a means of fungi entering the tree. Not infrequently *Fomes laricis* enters its host by this means. Mistletoe burls on Douglas fir are known to become infected with *Trametes pini*. A mistletoe burl on Alpine fir was found to be inhabited in one instance by *Pholiota adiposa* Fr. Meinecke (10, p. 58) refers to the mistletoe cankers of *Abies concolor* as offering an easy entrance to germinating spores of *Echinodontium tinctorium*. Burls on yellow pine, owing to their resinous condition, are seldom attacked by wood-destroying fungi. The bluing fungus, however, has been found by the writer in the distorted tissues of mistletoe burls on living yellow pine.

FIG. 25.—The soft spongy cortex of a mistletoe infection on lodgepole pine gnawed by rodents. This is a very common type of injury in mistletoe-infected trees.

GENERAL SUPPRESSION AND FUNGOUS ATTACK.

Aside from the fact that fungous enemies enter these conifers through broken branches, lesions, and burls caused by mistletoe, heavily infected trees are, owing to their weakened condition, more susceptible to fungous attack on any part—roots, trunks, or leaves. In the lake region of Idaho the larch of all ages and conditions is at present suffering from an epidemic of a needle disease, *Hypodermella laricis* Tub. It is observed that in practically every instance the needles of very old mistletoe brooms are first attacked, whereas those of the uninfected trees of particular age classes or exposures may ward it off for a longer period.[1] It is a common observation that in regions of heavy mistletoe infection (and nowhere is it better shown than in the forests of eastern and central Oregon and many parts of Idaho and Montana) many heavily infected trees are in a dead and dying condition. If these trees are carefully examined with reference to average healthy growth for the region, it will be found that they have died prematurely.

It has already been indicated that mistletoe is capable of causing the death of its host in some instances. The whole tendency of the parasite is to reduce the life functions of its host to the lowest point, and if death does not result from this cause alone the way is opened to various secondary agents, which may or may not attack vigorously growing trees. The gradual thinning out of the foliage of heavily infected trees and the appropriation by the brooms of much of the elaborated food materials must necessarily result in an unbalanced relation between the crown and the root system. Consequently, there may be a dearth of food materials for the latter, wholly inadequate to support its present extent. It may be naturally inferred that this results in the suppression of the roots or a dying off of the more extended members of the system. A close examination of a hundred or more windfalls of heavily infected Douglas fir, yellow pine, and larch in the regions above mentioned shows quite clearly that the horizontal and brace roots of these trees in most cases were badly decayed. Since few windfalls of the heavily uninfected trees of the same average age and size were observed in the same region, it may be inferred that a possible relation existed between the suppressing effects of the mistletoe and the decay in the roots. *Armillaria mellea* (Vahl.) Quél. was definitely associated with some of the decay in the roots. In most cases, however, owing to the absence of fruiting stages, the cause of the rot in the fallen trees could not be determined.

[1] *Hypodermella laricis* was first named and described by Von Tubeuf on the European larch (*Larix europaea*). This is the first note of its occurrence in North America. The fungus, characterized by its four clavate spores to an ascus, is very destructive and is the cause of considerable damage in the larch forests of the northwestern United States and Canada.

It is a well-known fact that wounds heal quickly in young or in strongly growing trees, principally due to the protection afforded by an abundant flow of resin. It may be assumed that trees having their life functions brought to a low ebb by excessive mistletoe infections, with resulting decrease in annual increment, will not be able to heal or protect their wounds as quickly as normal trees; hence, are more liable to infection. This may be one of the reasons why so many open burls are formed on infected larches. These open burls are seldom, if ever, healed, although the parasite in its tissues has long since died. There is a slight increase in the number of resin passages in early burl formations, but this is entirely offset by the early dying out of the bark of the burl exposing the wood. It is an observed fact, experimentally proved by the writer, that strongly suppressed yellow pine, larch, and Douglas fir do not as readily form traumatic wood or exude the normal quantity of resin on being wounded on any part as do normal, healthy trees. Such a tardy reaction to injury does not afford a ready antisepsis against the entrance of fungi which may attack these trees. Since turpentine orcharding is becoming more extensively practiced in the West it would be an interesting experiment to determine the relative flow of pitch from trees strongly suppressed by mistletoe and from those in a high state of health.

RELATION OF MISTLETOE INJURY TO INSECTS.

In the same manner that burls and other types of mistletoe injury on some conifers are open doors to fungi, they are found to afford a ready means of entrance for some species of forest-tree insects which do not in this region habitually attack vigorous unwounded trees. Old mistletoe burls on larches are almost invariably attacked by borers (figs. 23 and 24), and burls on yellow pine are, in the experience of the writer, quite as frequently infested by bark and wood boring beetles. In this connection a very curious and interesting phenomenon often occurs on young yellow pines from 10 to 20 years of age. An infection by mistletoe will have occurred, completely enveloping the trunk some 2 or 3 feet from the ground. The parasite having advanced somewhat each way from the point of original infection, the intervening space is attacked by *Dendroctonus valens* Lec. The combined influence of the beetle and mistletoe results in the complete infiltration with resin of the space between the two edges of the advancing mistletoe, so that the cambium dries out and dies. Strange to state, this does not always kill the tree. The crown goes on manufacturing food materials, being supplied with water through the inner wood of the girdled area. The elaborated food not being able to travel downward, since the cambial tissues of the entire circumference of the stem have been destroyed, is stored just above the

girdled area and initiates an abnormal swelling (fig. 26). The swelling continues to increase in size and weight, likewise all members of the crown, so that eventually the slender stem below can no longer support the overdeveloped crown and is broken down by the wind. A specimen in the laboratory shows the number of rings of the stem at the girdled area at the time it was cut to be eight, with a diameter of 1 inch. The swelling just above and within the same internode showed 15 rings, with a diameter of 3 inches. The same phenomenon is sometimes produced in yellow pine by *Peridermium filamentosum* Pk. When it is recalled that the cambium and the outer wood of the girdled area are actually dead, the length of time the crown continues alive is really remarkable.

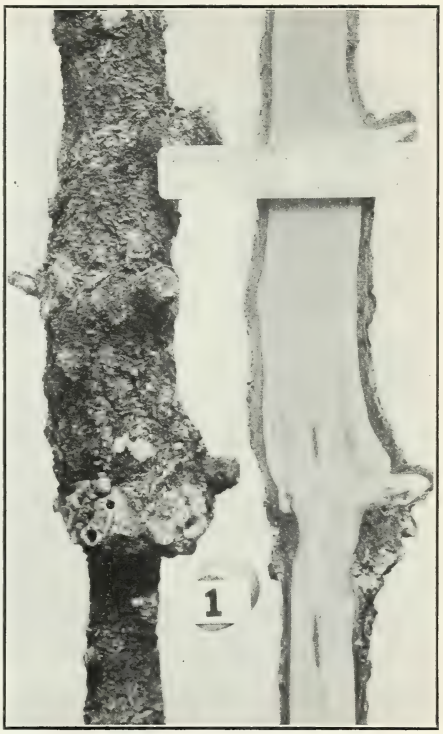

FIG. 26.—A young yellow pine, showing complete girdling of the stem by a combined attack of mistletoe and insects. The cambium is destroyed, but the crown remains alive and continues to elaborate food materials, which are stored just above the girdled area.

In point of general insect attack it has been noted that the beginning of an infestation may start with trees badly suppressed by mistletoe. The fact that trees heavily suppressed by mistletoe have a weak flow of sap causes them to be first selected by certain forest-tree insects. For this reason mistletoe areas form centers from which infestations may spread. Again, numerous infestations may start simultaneously over a wide territory, owing to the weakening of the trees by these parasites instead of from a few detached areas, as is often the case. This has been found particularly true in the case of yellow pine and the red turpentine beetle mentioned above. In all regions of heavy mistletoe infection of the Douglas fir, *Dendroctonus pseudotsuga* Hopk. is usually very abundant. This was the rule in the Whitman National Forest, Oreg., and though the numerous dead trees of this species in the forest were undoubtedly the result of an immediate attack by the beetles, their work was hastened, it seemed, by the serious mistletoe suppression which was exhibited by most of the dead trees. During the season

of 1914, a large number of badly suppressed Douglas firs on the foothills bordering the Clark Fork (Missoula River) Valley have died from a combined attack of mistletoe and beetles. Most of these trees, which supported scarcely a single normal branch, had the bark of limbs and trunk almost entirely removed by woodpeckers in their search for the beetle before the leaves were entirely dead. The few uninfected Douglas firs of the same region have not been attacked by the beetles.

The branches of large mistletoe brooms on yellow pine and Douglas fir from which the parasite has entirely disappeared are very

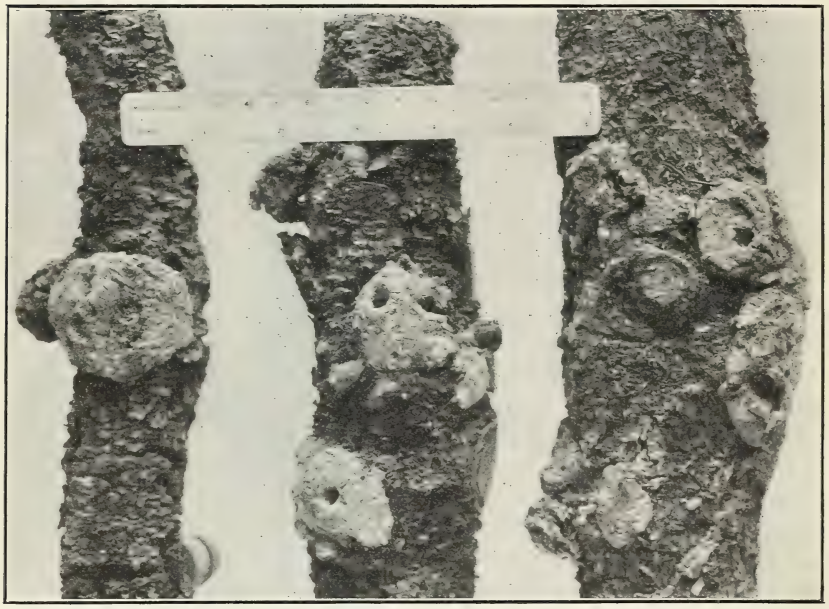

FIG. 27.—Seats of original mistletoe infection on two living branches (in center and at left) of mistletoe brooms on yellow pine infested with bark beetles. No other part of the broom or tree was attacked. Main stem of young living yellow pine (at right) attacked by bark beetles at the seat of an old mistletoe infection.

frequently found infested with bark beetles (fig. 27), while the trunk and normal branches of the trees are entirely free from attack.

INFLUENCE OF MISTLETOE INJURY ON THE SEED PRODUCTION OF THE HOST.

Germination tests of seeds of yellow pine taken from mistletoe-infected trees show that the percentage of germination is considerably lower than is the case with seeds taken from normal trees (12, p. 7). Experiments conducted by the writer with seeds taken from cones produced on very old mistletoe brooms of Douglas fir, larch, and lodgepole pine showed a germination on an average of 10 per cent below that of seed taken from uninfected branches of

the same trees. Given the general average percentages of germination of 30 for the former and 40 for the latter, it seems that either from exhaustion of stored materials or tendencies toward abnormal seed production in general the uninfected branch, though suppressed, is still capable of producing a higher quality of seed than the broom. Whether this would be true in the case of young, vigorous brooms is doubtful. Seeds from the uninfected branches of the same strongly suppressed trees used in the above experiment gave a general average of 15 per cent below that of seeds taken from vigorous uninfected trees of the same age, species, and habitat. The percentage of 65 for the uninfected and 40 for the infected shows quite clearly that suppression by mistletoe causes a serious falling off in the quality of the seed of its host.

The experiment was conducted in the following manner. Collections of cones were made from each of five strongly suppressed and five uninfected trees of all three species. This included one collection from the brooms, one from the uninfected branches of each of the suppressed, and one collection from each of the uninfected trees; in all, 45 different collections. One hundred seeds were extracted from each collection and germinated in sand at an average temperature of 35° C. Counts were made at different intervals during the progress of the test, which was continued for 90 days. Considerable difficulty was experienced in procuring the required number of seeds for all conditions, owing to the sterility of the cones on the old brooms. With the increasing age of the broom the seed production falls off, until, as it is with most species, no cones are produced at all. Seeds from recently formed brooms were not tested. It is supposed that they would show a higher percentage of germination. The cones on badly suppressed trees are very often aborted, with shriveled, undeveloped sporophylls, and are frequently infested by cone beetles and cone worms. Seeds, if produced in such cones, are usually below the normal size. A study of microtome sections of the staminate flowers from heavily infected lodgepole pine showed that there was a reduction in the number of pollen mother cells. The staminate flowers when compared with those of normal trees of the same age and condition were found to be uniformly smaller. The sporophylls on the more fertile or convex side of the young pistillate cones very frequently bore only one ovule (megasporangium), a condition not observed in cones from healthy trees.

HOST AFFINITIES IN RELATION TO SILVICULTURE.

For practical purposes the following statements on the host requirements of the mistletoes of coniferous trees will be found to be of some interest with regard to the silvicultural management of forests.

Razoumofskya douglasii (Engelm.) Kuntze is of economic importance only on the Douglas fir. The affinities of the very small and rare forms of Razoumofskya on spruce and fir,[1] described by Engelmann (6, p. 253) under the name of *Arceuthobium douglasii* var. *microcarpum* for the former host and *A. douglasii* var. *abietinum* (3, v. 2, p. 106) for the latter, are not definitely established. In point of time of blooming and seed maturity, it coincides with that of *Razoumofskya douglasii* for northern regions, and their form and color are quite similar, especially the color of the staminate flowers. These small plants, together with the Douglas fir mistletoe, are the only members of the genus exhibiting a pronounced color of the lobes, which are a bright, deep purple. Until cross-inoculation experiments are perfected, these particularly small mistletoes on spruce and fir may be considered wholly unimportant from a silvicultural standpoint. For the sake of convenience, they may be placed with the Douglas fir mistletoe and the whole designated as the *Pseudotsuga-Abies-Picea* group, characterized by their small size and colored flowers. *Razoumofskya laricis* Piper, the most universally distributed and probably the most injurious of the entire genus, is associated with the western larch. This species in a single instance has been collected by the writer on lodgepole pine near Missoula, Mont. It is a significant fact that this infection is not vigorous and appears to be dying out. *R. americana* (Nutt.) Kuntze is more strictly associated with the lodgepole pine, but is the cause of serious damage to the jack pine (*Pinus banksiana*) where these two species approach each other in Canada. *R. tsugensis* Rosend., as far as observations in the field have gone, is confined to the hemlocks.

The remaining species of importance may be divided into two main groups, a fact that has not been heretofore set forth, viz, those associated with the soft or white pines and those attacking the hard yellow pines. It seems that the members of one group are not in a single instance associated with the hosts of the opposite group. The former group includes the following species and hosts: *Razoumofskya divaricata* (Engelm.) Coville on the nut or piñon pines, *P. edulis* and *P. monophylla* (6, p. 253); *R. cyanocarpa* A. Nels. on *P. flexilis* (4, p. 146), *P. albicaulis*, and *P. monticola*. *Pinus monticola* has not been previously reported as a host for these parasites. *Pinus strobiformis*, the Mexican white pine, is reported (11, p. 65) as the only host of *R. blumeri* (A. Nels.) Standley. The second group may be included by the two-form species: *R. campylopoda* (Engelm.) Piper and *R. cryptopoda* (Engelm.) Coville. The former is principally injurious to *Pinus ponderosa*, but is common on *P. attenuata* (7, p. 366; 13) and *P. jeffreyi* (10, p. 38). The latter is likewise an injurious parasite on

[1] *Abies concolor* is also host for *Phoradendron bolleanum* (Seem.) Eichl. (5, p. 193).

P. ponderosa, but occurs on *P. jeffreyi* (5, p. 192), *P. arizonica* (2, p. 243), and *P. mayriana* (2, p. 243). *R. campylopoda* has recently been collected by the writer near Coeur d'Alene, Idaho, on *P. contorta*. Sparingly distributed throughout the Northwest are some large forms of Razoumofskya on Abies. Plants collected by the writer on *Abies grandis* and *A. concolor* are apparently the same as that described by Engelmann (3, v. 2, p. 106) on the former host under the name *Arceuthobium occidentale* var. *abietinum*. Although it would probably be better on morphological grounds to refer this form to *R. campylopoda* (Engelm.) Piper, as Engelmann's *Arceuthobium occidentale* is now named, owing to its seeming close affinity to the genus Abies and the absence of cross-inoculation data it could well be raised to specific rank. These mistletoes in point of morphology are in great contrast with the small forms on Abies previously mentioned. They may be considered typical of a group of large forms occurring only on Abies.

From the foregoing, it seems possible that the members of the genus Razoumofskya may be arranged in a series of natural groups according to their host relationships. It is also interesting to note that the largest, the longest lived (both cortical and aerial parts), and the most strictly parasitic forms are associated with the hard or yellow pines. These pines exhibit anatomically a high differentiation. This may throw some light on the nutrient relation of some mistletoes to their hosts; also their family peculiarities.

SUGGESTIONS FOR CONTROL.

It is clear from the foregoing pages that the damage to forest growth by the mistletoes of coniferous trees in the Northwest is of sufficient importance to receive the attention of every forester. Steps should be taken in all logging operations, where local problems of economy do not interfere, to make a beginning of the eradication of mistletoe by marking every infected tree for cutting. In some cases it would seem advisable to introduce into the contract a special clause dealing wholly with mistletoe-infected trees. The most injurious of the mistletoes of the genus Razoumofskya on coniferous trees, as indicated, are in the main confined to their own particular hosts or to special groups; hence, it is not advisable to establish in mistletoe regions pure stands of a species much subject to attack. In this respect the problem of the control of mistletoe is similar to that of forest-tree fungi. Mistletoes being light-loving plants, close stands should be maintained as much as possible on all exposed parts of the forest. For the same reason rims of canyons and all exposed areas, such as the borders of bench lands, natural parks, shores of lakes, etc., should be protected with species which are not usually subject to the ravages

of mistletoes (Pl. IV, fig. 2). In this class would fall the firs, spruces, arbor vitæs, cedars, junipers, and yews. If this can not be done, owing to certain requirements by these species on soil and climate, the stand should be composed of as many different species as possible.

Aside from reasons already set forth, isolated seed trees heavily or even slightly infected by mistletoe should not be retained. The vigor of the parasite on the parent tree will become greater, owing to its response to open and well-lighted conditions. Reproduction under the tree and in its near vicinity, if of the same species, will readily become infected. The same will be true of seed plats. The force developed within the mature seed capsule of these mistletoes and exerted in the expulsion of the seed is a factor of great significance for the spread of the parasite. It has been demonstrated in the case of one species that this force is sufficient, starting at an elevation of 8 feet on the level, to carry the seed a distance of over 66 feet. In addition to the forcible expulsion of its seeds by the parasite, strong wind is an important factor in seed dissemination. In one instance seeds of the larch mistletoe were collected in number from the roof of a cabin one-fourth of a mile away from the nearest infected tree. This is not at all extraordinary, in view of the fact that the larches of the region are very tall and are heavily infected in the crown. Also strong winds are frequent during the period of seed maturity. Birds and animals play a minor rôle in the distribution of the seeds of these mistletoes.[1] In the present instance, however, the seeds adhered to the substratum in the usual and normal manner and could not have been transported in such numbers by any other means than strong wind.

In view of the fact that strong air currents are factors in the dissemination of the seeds, some consideration should be given to the topography and prevailing winds of a region where mistletoe abounds, as influencing the selection of seed plats (if such methods are employed), the placing of strip cuttings, and even of nursery and transplant beds. On a previous page, the tender age at which coniferous seedlings are liable to infection by mistletoe is indicated, so that the above statement regarding nursery sites is not merely a conjecture. Since considerable time elapses between the actual penetration of the primary sinker and the time the infection becomes conspicuous, three years in some instances, it is quite possible for

[1] In Bulletin 317 of the U. S. Department of Agriculture, page 24, the writer published a footnote on the rôle of birds and animals in the distribution of the seeds of these mistletoes. Since this publication was issued additional observations show that the seeds are probably more widely distributed by this means than was formerly believed. A rumor has been long extant that grouse feed upon the mistletoes. This has recently been verified by the writer by finding in the crop of a grouse the mature seeds and plants of the Douglas fir and larch mistletoes. Mr. Donald Morrison, an old, experienced hunter residing in the mountains near Missoula, states that grouse in the late fall, with the coming of the winter snows, make a practice of congregating in the dense houselike brooms of the Douglas fir mistletoe. Mr. Morrison states quite positively that these birds feed upon the plants and mature seeds of these parasites when other forms of food become scarce.

young infections on nursery stock to escape detection. Accordingly, young infected seedlings may become a means of distributing and establishing the parasite in plantations generally, not only locally but to far distant regions, when growing stock is shipped either for experimental purposes or for permanent plantings. That this is possible is shown by the discovery in the planting areas near Wallace, Idaho (Coeur d'Alene National Forest), of a yellow-pine seedling showing a very recent infection of mistletoe. Since the plantings were made on a widely denuded area and no yellow-pine mistletoe is as yet known to occur in the immediate region, it seems that the seedling must have become infected while at the home nursery at Boulder, Mont., where this mistletoe occurs. In view of the fact that there is a very grave danger of transporting agents injurious to forest growth, either fungous diseases or mistletoe, by sending nursery stock to distant parts of the country, the need of strict sanitation in the neighborhood of forest-tree nurseries can not be overemphasized. Whenever new nursery sites are planned in or near forests, a close pathological survey should be made of the surroundings, and trees diseased or suppressed from any cause whatever should be cut out. This should be done also where nurseries are already established.

The influence of the physical type on the severity of attack should receive considerable attention in any plan of management of forests in mistletoe regions. Forest Assistant Gilkey, in a report on the western larch of the Whitman National Forest, states that "a total of several hundred trees in various parts of the forest shows 79 per cent of the larch to be attacked on the dry-slope type, with only 27 per cent on the more moist sites." The writer's own investigation in the same forest shows an even greater difference between the moist-valley type and the more exposed slopes, which was 87 per cent for the latter and 15 per cent for the former. The severity of the infection on yellow pine and Douglas fir in other regions likewise shows wide extremes as influenced by elevation and exposure. Mr. E. E. Hubert, of the Laboratory of Forest Pathology, reports from extensive observations during a reconnoissance of the lodgepole pine in the Big Hole Valley, Mont., that the most favorable sites for mistletoe are exposed dry ridges and south slopes, where the infection ranges from 50 to 70 per cent of the stand. In the valley type the percentage of infection was much lower.

In view of the fact that all economic species so far observed are subject to attack at any age, it is hardly possible to establish an age at which infection becomes so serious as to interfere with the merchantability of the host. In regions of heavy mistletoe infection it would be quite impossible, for the reason that there is a much greater chance for all age classes to become infected. In numerous in-

stances, however, it is noted that in some regions Douglas fir, larch, and lodgepole pine first become conspicuously infected at sapling or pole size; that is, it has required several years for earlier infections to become prominent. In any case, the matter turns on the time of life at which a tree becomes infected. If seriously infected before pole size is reached, the whole tree will in all probability be a cull and a menace to the forest. If infected during or after pole age, the tree may furnish some merchantable material, but will mature far in advance of uninfected trees of the region. Trees infected during early maturity may not be seriously influenced by the parasite except that their life functions may be slightly changed by brooming and breakage of branches, thus hastening the period of decline. Cutting old and suppressed mistletoe trees is, of course, a saving in several ways, not only to the future forest, but it is getting the best out of a rapidly declining forest capital. Their destruction, however, does not mean that a great advance is being made in eradicating the mistletoe from the region. It simply lessens the chance of infection for a time. Cutting the old and merchantable infected trees and leaving the younger unmerchantable but infected growth will not answer the purpose of control in regions of heavy infection. Very frequently the removal of only the more merchantable mistletoe trees causes the parasite on the trees that are left to develop more vigorously. Numerous observations show that infected trees of various ages succumb very rapidly to the parasite after a certain percentage of the stand has been cut out. For this reason marking the most seriously infected trees for cutting, with the prospect of the least infected reaching a normal maturity or a state of high merchantability, should in many regions be discontinued. The only plan left, then, in many regional units of infection is to practice heavier marking than hitherto employed, or, better still, clean cutting. It is believed that a close survey of the forests of each district will result in the discovery that there are units or centers of great infection either for one species of mistletoe or for different species.

Instances of great regional infection for the Northwest have already been indicated. Strange to say, in some cases these centers of infection are quite sharply defined. It seems entirely possible that if these regions were carefully studied and mapped as to the possible environmental factors governing the vertical and horizontal distribution of the parasite, much practical knowledge would result. If the region should be accessible, the sales policy could be modified, with strong emphasis on the control of the mistletoe, and the knowledge already gained from a detailed study of the region should be available for future forest management. It must be remembered that the great injury now exhibited by forest growth is the accumulation of many years of unhindered activity by these

mistletoes. Through a proper appreciation of the need of adopting control measures in all sales areas where the percentage of infection is high and in all replanting projects in mistletoe regions, with the free-use privileges of mistletoed trees and the cutting of all infected growth in the vicinity of forest-improvement stations, a good beginning could be made toward the eradication or the lessening of the ravages of these parasites.

SUMMARY.

The conifers in the Northwest most subject to injury by mistletoes of the genus Razoumofskya are *Larix occidentalis*, *Pinus contorta*, *Pseudotsuga taxifolia*, and *Pinus ponderosa*. In the order of the above-named hosts the mistletoes most responsible for the greatest damage are *Razoumofskya laricis*, *R. americana*, *R. douglasii*, and *R. campylopoda*.

The general nature of the injury by these mistletoes is expressed in a gradual reduction of the leaf surface of the host, which causes a great reduction of growth in height and diameter.

New infections take place only through the agency of a germinating seed, which reaches the point of infection through the natural expelling force of the seed capsule, which may be made more effective in point of distance traveled by the aid of strong winds, by falling from branches above after they have been loosened from their original resting place by rains, and by animal life.

Trees of all age classes are liable to infection provided the mistletoe seeds fall on parts of the host not yet protected by the mature cortex. The parasite may spread from the original point of infection into older cortical tissues, which are not liable to infection from without. The spread of the cortical stroma in the reverse direction from the line of growth of the branch may continue until the outer cortex becomes too thick for the aerial shoots to penetrate it. After this, the cortical roots become suppressed and eventually die, or they may become wholly parasitic.

Excessive mistletoe infection of the lower branches of a tree may cause the upper portion of the crown to die, giving rise to the phenomenon commonly called staghead or spiketop. Severe infection throughout the entire crown often results in the death of the tree. Young seedlings from 3 to 6 years old are often killed within a comparatively short time after infection.

Infection on the branches in practically all cases causes the formation of large brooms, which seriously interfere with the life function of the tree. The same is true in the case of infection on the trunk, whereby burls are formed.

The weakening effect of the formation of burls and brooms by mistletoe on forest trees is often responsible for serious depredations by fungi and forest-tree insects.

In point of quality and quantity the seed-producing capacity of trees suppressed by mistletoe is far below that of normal uninfected trees.

Mistletoe can be controlled. It is suggested that a beginning may be made in its eradication or in the reduction of the ravages caused by these parasites by working along the lines indicated in the last section of this bulletin.

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